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ORIGINAL PAPER

Short-term effects of cattle browsing on tree sapling growth in mountain wooded pastures

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Abstract Browsing by livestock has been identified as an important factor preventing tree regeneration in wooded pastures. Two field experiments were performed to investigate the effects of cattle browsing on tree sapling growth in a mountain-wooded pasture. Two size classes (ca. 12–17 cm and 41–59 cm) of each of 4 species (*Picea abies*, *Abies alba*, *Acer pseudoplatanus* and *Fagus sylvatica*) were exposed to zero, low and high grazing intensities. We measured the proportion of saplings browsed and the effect of browsing on growth. A mowing treatment within the zero grazing intensity treatment showed no significant effect on sapling growth. One percent of the large saplings but 25% of the small saplings escaped browsing. Saplings were better protected when surrounded by taller vegetation. The proportion of saplings browsed was not significantly different among species although evergreen tree saplings lost a larger proportion of biomass than deciduous species when browsed. Under grazing, average current-year shoot production and total aboveground biomass of all species were significantly reduced. Browsing effects tended to be smaller at the lower grazing intensity. Because the deciduous species were least reduced in aboveground growth, especially under the low grazing intensity, we conclude that at least in short-term, deciduous species are less affected by cattle browsing.

Keywords *Abies alba* · *Acer pseudoplatanus* · *Fagus sylvatica* · *Picea abies* · Grazing intensity · Silvopastoral system · Tree regeneration

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Introduction

In recent decades, agricultural intensification has reduced the area occupied by ancient wooded pastures in temperate Europe. Several examples remain, including in the Swiss Jura Mountains. To conserve these landscapes, trees and herbaceous vegetation must be able to continue to coexist in a dynamic equilibrium under livestock grazing (Vera 2000; Archer et al. 2001). Worldwide, land managers are increasingly interested in combining silviculture and agriculture to re-establish silvopastoral systems, in order to preserve biodiversity and provide socio-economically viable options for

local farmers (Etienne 1996; Hobbs and Yates 2000; Teklehaimanot et al. 2002). Young trees are vulnerable to browsing and understanding the factors affecting their establishment is of concern (Gillet and Gallandat 1996; Sharrow et al. 1992). If grazing intensity is too high, trees fail to regenerate and wooded pastures evolve towards grassland ecosystems. In absence of pastoral activities, they evolve towards climax forest ecosystems. Livestock foraging behaviour in grasslands and rangelands has been an area of intensive research (Rook et al. 2004) but the effect of livestock on biomass of woody species in the herb layer has received much less investigation.

Cattle generally select for a grass-based diet with a high digestibility and high N and P concentrations (Ayantunde 1999; Mayer et al. 2003). Due to the high levels of difficult-to-digest lignin and secondary metabolites, most woody species are generally avoided by cattle (Gordon 2003). However, browsing by livestock has been identified as an important factor preventing tree regeneration in wooded pastures (Papachristou and Papanastasis 1994; Lehmkuhler et al. 2003; Bakker et al. 2004; Allcock and Hik 2004). The consumption of woody plants increases when high quality forage is unavailable, often under dry weather conditions (Holechek et al. 1982; Owen-Smith and Cooper 1987; Fritz et al. 1996) or in late summer (Leloup et al. 1996). Tree sapling damage and mortality also increases with grazing pressure (Pitt et al. 1998; Hall et al. 1992), a result of increased consumption or trampling. In the wooded pastures of the Swiss Jura Mountains, four common tree species, including two conifers (*Abies alba* and *Picea abies*) and two deciduous species (*Acer pseudoplatanus* and *Fagus sylvatica*), co-occur between an altitude of 800 and 1,200 m. *Picea abies* is currently dominant. Little is known about the selectivity of domesticated cattle among these different species and the responses of saplings to browsing. Apparency, i.e. the probability that an individual plant will be discovered by its enemies (Feeny 1976), is not only dependant on the characteristics of the plant itself, e.g. plant size, foliage abundance and duration (Welch et al. 1991; Zamora et al. 2001; Renaud et al. 2003) but also on the relative abundance and nature of neighbouring plants (Milchunas and Noy-Meir 2002). Coniferous species are likely to be more apparent than deciduous species, but might be avoided by cattle because of their lower leaf nitrogen content (Pagès et al. 2003) and stiff, tough needles. Furthermore, deciduous species have a greater ability for compensatory growth after browsing damage because conifers store most of their nutrients in the needles, whereas deciduous species have greater stores in roots and old wood (Chapin et al. 1990; Hester et al. 2004).

Livestock will consume not only saplings but also the surrounding vegetation. Tree sapling success may be strongly influenced by the intensity of competition from herbaceous vegetation (e.g. Gill and Marks 1991; Pagès et al. 2003). Livestock may, therefore, have an indirect positive effect on tree sapling establishment at sites where grazing reduces the ability of grasses to competitively exclude less-preferred woody seedlings (Archer 1995).

The effect of cattle on the growth of tree saplings of different species under varying grazing intensities has, to our knowledge, never been quantified in wooded pastures. The relative importance of the direct (biomass removal) and indirect (reduced competition) effects of cattle browsing on sapling growth is not well known. In this research, our first objective was to quantify direct browsing effects. We investigated if the probability of being browsed depended on species, sapling size, grazing intensity or the height of the surrounding vegetation. Furthermore, we quantified the reduction in sapling growth due to cattle browsing and examined differences in sapling growth between species, sapling sizes and grazing intensities. Our second objective was to assess the strength of indirect grazing effects using a mowing experiment.

Materials and methods

Study site and focal species

Two field experiments were conducted over the growing season of 2003 in two adjacent paddocks of a site called 'La Petite Ronde' (6°27′26″ E, 46°56′22″ N, altitude 1,125 m a.s.l.) at

Les Verrières in the Swiss Jura Mountains, which is rented by the Agroscope-Changins and Liebefeld-Posieux Research Institutions (Switzerland). The site has been grazed for more than 100 years and a rotational grazing system was established in 2000. In 2003, between May and October, each paddock was grazed four times for approximately 15 days by a herd of 22 18-month-old steers. The year 2003 was particularly hot and dry with a mean June temperature of 18±2.2 (SD) °C (1994–2003 mean June temperature 13±2.2°C) and a total of 980 mm of precipitation (1994–2003 mean 1,607±548 mm). The most common herbaceous species were *Festuca rubra*, *Agrostis capillaris*, *Cynosurus cristatus*, *Alchemilla xantochlora* aggr., *Prunella vulgaris*, *Trifolium repens*, *Centaurea jacea* s.l. and *Ranunculus acris friseanus* (nomenclature follows Lauber and Wagner 2000). The site was surrounded by a mixed forest and tree saplings were observed in adjacent paddocks. However, all naturally established tree saplings in the paddocks had been mechanically removed by the farm managers in former years.

We used the four most common tree species of the wooded pastures of the Jura Mountains: the evergreen species *Picea abies* and *Abies alba* and the deciduous species *Acer pseudoplatanus* and *Fagus sylvatica*. Tree saplings of two sizes were obtained from a local nursery (Lobsigen, Switzerland) and were transplanted into two paddocks exposed to different intensities of grazing.

Experimental design

Two experiments were carried out: a browsing experiment tested for direct browsing effects and a mowing experiment for indirect effects. The height and diameter (at 1 cm above root collar) of all experimental saplings were measured before transplantation in mid-April 2003 (Table 1). 'Small' and 'large' sapling size classes were defined by height rather than age. Eighteen additional saplings of each species and size class were measured, dried at 60°C for 48 h, and weighed. These data were used to construct a linear regression model for each species in order to estimate the initial aboveground biomass of the experimental saplings (Table 1). Saplings that died due to transplantation shock or late frost (2 small and 3 large *Abies*, 3 small *Picea*, 19 small *Acer* and 14 small and 6 large *Fagus*, total of 47 of 512 saplings) were replaced one week before cattle arrived in both paddocks on 27 May 2003.

For the browsing experiment, trees were transplanted into two paddocks of different grazing intensities. Paddock 1 (3.3 ha) had a high grazing intensity with a stocking rate of 128 Livestock Unit Days ha^{-1} and paddock 2 (4.5 ha) had a lower grazing intensity with a stocking rate of 94 Livestock Unit Days ha^{-1} (1 Livestock Unit = 600 kg cattle weight). Sixteen blocks (8 × 8 m) of 8 saplings were randomly placed into each paddock (total of 256 saplings) (Fig. 1a). Within each block, saplings (4 species × 2 sizes) were randomly assigned to positions and planted at the mid-points and corners of each block (Fig. 1a). This resulted in a minimum distance of 4 m between saplings. Mean vegetation height (±SE) before the arrival of cattle was 11.5±2.8 cm in paddock 1 and 11.8±2.9 cm in paddock 2. After two rotation periods, mean vegetation height was 7.6±1.8 cm in paddock 1 and 8.9±1.9 cm in

Table 1 Age, initial height, diameter and dry mass (mean ± SE) of the small and large transplanted tree saplings (N = 128 per species)

		Age (years)	*h* (cm)	*d* (cm)	DM (g)	logDM =	R^2
Abies	Small	3	12.6±2.6	0.27±0.1	0.69±0.12	$-0.156 + 0.732 \times \log(d^2h)$	0.905
	Large	6	40.6±7.2	1.13±0.04	34.9±21.1	$0.035 + 0.859 \times \log(d^2h)$	0.865
Picea	Small	2	12.3±2.4	0.23±0.01	0.67±0.38	$-0.031 + 0.900 \times \log(d^2h)$	0.875
	Large	5	50.6±8.5	1.13±0.03	50.6±23.1	$0.256 + 0.790 \times \log(d^2h)$	0.910
Acer	Small	1	18.6±4.6	0.31±0.01	0.42±0.19	$-0.543 + 0.604 \times \log(d^2h)$	0.810
	Large	3	58.8±9.4	0.65±0.02	4.1±1.6	$-0.138 + 0.659 \times \log(d^2h)$	0.798
Fagus	Small	1	16.8±3.7	0.34±0.01	0.54±0.33	$-0.556 + 0.838 \times \log(d^2h)$	0.886
	Large	3	57.1±8.5	0.75±0.02	6.7±2.4	$-0.288 + 0.753 \times \log(d^2h)$	0.700

Regression formulas used to estimate initial aboveground dry mass (DM, g) from height (*h*) and basal diameter (*d*) measures on the four species and two size classes. For all models, N = 18 and $P < 0.001$

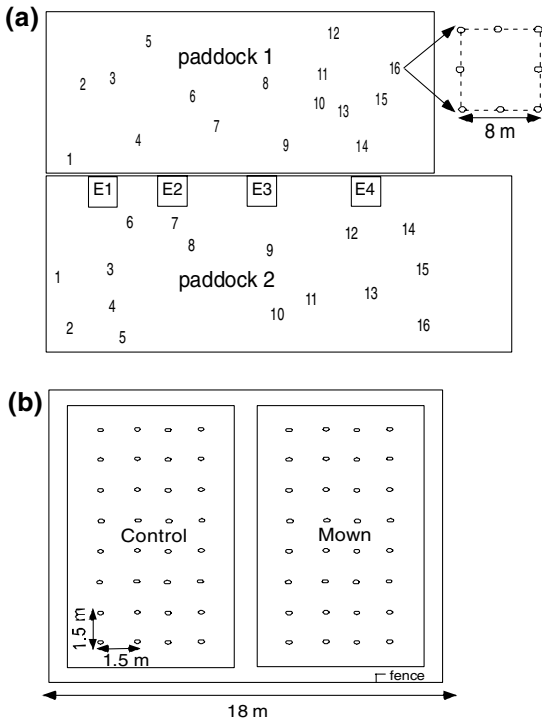

Fig. 1 (**a**) Experimental layout: 16 blocks were randomly located in paddock 1 (high grazing intensity) and paddock 2 (low grazing intensity). Each 64 m^2 block (shown in expanded view) consisted of 8 saplings (○ = sapling) randomly assigned to positions within the block. Four exclosures (E) were erected in paddock 2. (**b**) In each of the exclosures, saplings were randomly assigned to positions within plots

paddock 2. The mean aboveground dry mass in July was 118 g m^{-2} for paddock 1 and 125 g m^{-2} for paddock 2. The factor ''grazing intensity'' could not be replicated due to logistic constraints and the paddock and grazing intensity effects are therefore confounded. However, we believe that the grazing intensity effect is much larger than the paddock effect as the two paddocks were adjacent and similar in vegetation, slope and soil type (Vandenberghe unpublished data).

For the mowing experiment, four 15.5 m by 18 m exclosures (used as statistical blocks), were erected in paddock 2, adjacent to the border with paddock 1 (Fig. 1a). Each exclosure was split into two plots of 13.5 m by 7.5 m surrounded by a 1 m buffer zone: in a randomly selected plot, vegetation was mown; the other served as a control (Fig. 1b). Each plot contained 4 individual saplings of each combination of species and size class (4 species × 2 sizes × 4 replicates: 32 saplings) randomly assigned to positions. A total of 256 saplings were transplanted (32 individuals × 2 plots × 4 exclosures). In the mown plots, vegetation around the saplings was cut to about 3 cm with a grass hand-mower and removed on 16 May, 30 May, 4 June, 25 June and 15 July. In the control plot, mean vegetation height (±SE) in July was 15.6±3.0 cm and mean aboveground dry mass was 360.5 g m^{-2}.

Data collection

In the browsing experiment, each sapling was examined in the field and scored as browsed or unbrowsed after each grazing period. The height of the vegetation surrounding each sapling was measured before (HB) and after (HA) the first grazing period with a herbometer (Mosimann et al. 1999). A plastic sheet (30 × 30 cm, 344 g) was lowered onto the canopy along a plastic rod and the height at which it came to rest was used as a measure of overall vegetation height. Vegetation height was measured at 4 points adjacent to each sapling in the cardinal directions and averaged. The absolute and relative reductions in vegetation height ($\Delta H = [HB–HA]$ and $\Delta H_{rel} = \Delta H \times HB^{-1}$) were calculated. The saplings of the browsing experiment were harvested on 4–5 August 2003, i.e. after two grazing periods of 14 days and 17 days, respectively. All saplings were cut at the root collar and scored as either dead or alive, based on the presence of green fibres under the cortex. Live saplings were separated into new growth and previous years' growth. The parts were oven-dried for 48 h at 60°C and weighed. Saplings that were pulled out by cattle (4% of the large and 22% of the small saplings) were scored as browsed but excluded from growth analyses.

Saplings of the mowing experiment were harvested on 15–16 August 2003. Sapling survival was scored and the final dry weight of live saplings was calculated as in the browsing experiment. One small sapling of each of *Fagus* and *Acer* could not be relocated and one large *Abies* was browsed by roe deer (*Capreolus capreolus*) and excluded from the analysis.

We focussed on two measures of sapling growth: (1) NG: relative new growth, calculated as the ratio of current-year shoot biomass over initial biomass and (2) BC: biomass change, calculated as the ratio of final over initial biomass. Sapling survival at the time of harvest was not analysed as we expected sapling death to continue due to browsing stress.

Statistical analyses

All data were analysed with R, version 2.1.1 (R Foundation for Statistical Computing 2004). We used mixed-effects models using blocks as random factors to account for within-paddock variability. Individual trees, clustered within blocks, were treated as independent sampling units since we assumed that the distance of 4 m between the saplings was sufficient to ensure independence with regard to the probability of being browsed.

A logistic regression was performed to test the effects of species, grazing intensity and size class on the probability of being browsed. Estimations were performed using generalised linear mixed-effects models estimated by maximum likelihood procedures (glmmML, Broström 2005). Likelihood ratio tests were applied to test significance of predictor variables. The complete model with 3 fixed factors and all pairwise interactions could not be estimated because the number of parameters was too large. The interaction terms were therefore tested separately, adding each of them to a model including only statistically significant main effects.

The relationships between predictor variables ''overall vegetation height'' (HB), ''absolute height reduction by grazing'' (ΔH), ''relative height reduction by grazing'' (ΔH_{rel}), ''grazing intensity'' (G) and ''size class'' (S) and the response variable ''probability of a sapling being browsed during the first grazing period'' were tested using glmmML procedures. We tested all pairwise interactions independently. Species was excluded because no significant species effect on browsing frequency was found in the previous analysis.

We tested for an effect of grazing intensity and size class on NG and BC. Sapling growth was analysed separately for each species because growth rates vary between species. Response variables were log-transformed to reduce heteroscedasticy (log (NG + 1) and log BC) and a normal distribution was assumed. Analyses were conducted using linear mixed-effects models (LME, Demidenko 2004) fitted by likelihood maximization. The use of LME models is more reliable than conventional ANOVA when analysing unbalanced data (Pinheiro and Bates 2000). Significance of the predictor variables was tested by comparing the fit of full and reduced models using likelihood ratio tests.

We tested for a mowing effect on NG and BC with mowing treatment, size class and their interaction as fixed predictors, using LME models and likelihood ratio tests as described for the browsing experiment. Exclosures were treated as a random factor.

Finally, in order to quantify the degree of growth reduction under grazing we combined data from the two experiments. We compared the NG and BC for saplings exposed to grazing to those in exclosures. We built a new predictor variable, grazing intensity, with three categories: zero, low and high. Given there was no detectable mowing effect, we included all saplings within exclosures at the zero grazing level. As previously, we used LME procedures on log (NG + 1) and log (BC). Blocks (browsing experiment) and exclosures (mowing experiment) were combined and used as random factors.

Results

Browsing experiment

After the first grazing period, 66% of the saplings were browsed under low grazing intensity against 78% saplings under high grazing intensity (L-ratio = 5.28, df = 1, $P = 0.022$). The browsing frequency between large (98%) and small saplings (46%) differed significantly (L-ratio = 108.1, df = 1, $P < 0.0001$) (Fig. 2a). No differences between species were found (L-ratio = 4.37, df = 3, $P = 0.22$). Few small *Fagus* saplings were browsed in the paddock with the lower grazing intensity but the interactions species × grazing intensity (L-ratio = 4.36, df = 3, $P = 0.22$) and

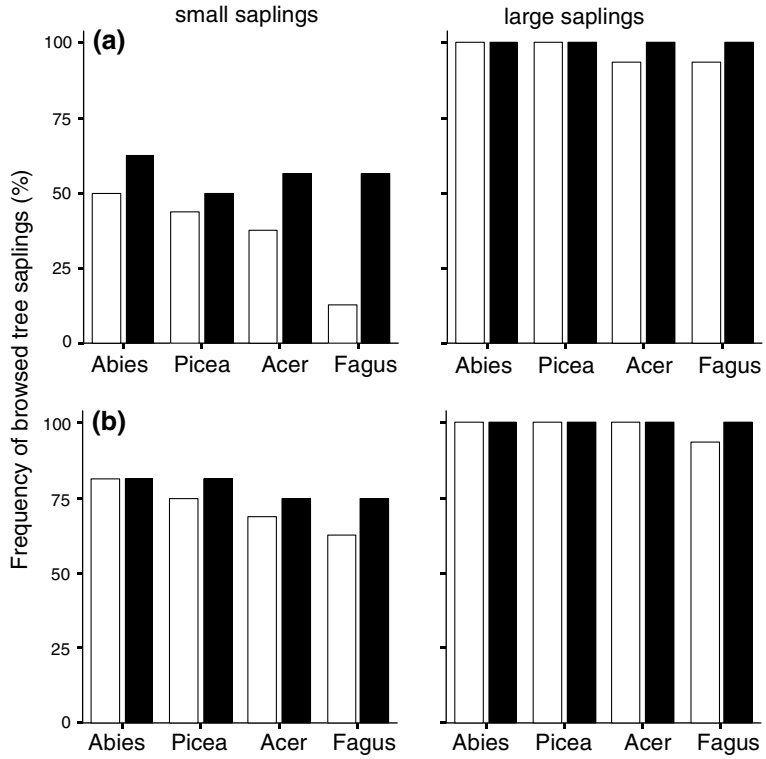

Fig. 2 Percentage of saplings browsed after the (**a**) first and (**b**) second grazing period for each tree species, size class and level of grazing intensity (*white bars*: low grazing intensity, *black bars*: high grazing intensity)

grazing intensity × size were not significant (L-ratio = 1.32, df = 1, $P = 0.25$). After the second grazing period, the proportion of tree saplings browsed under low grazing intensity (85%) and high grazing intensity (89%) no longer differed significantly (L-ratio = 1.0, df = 1, $P = 0.32$) (Fig. 2b). The difference between tree size classes remained significant (Fig. 2b; 99% of large vs. 75% of small saplings, L-ratio = 41.2, df = 1, $P < 0.0001$). The four species were browsed at approximately the same ratio (L-ratio = 2.37, df = 3, $P = 0.49$).

The probability of a sapling being browsed decreased with increasing height of surrounding vegetation (HB: L-ratio = 6.55, df = 1, $P = 0.01$) (Fig. 3). In contrast, the probability of a sapling of being browsed was not significantly related to either absolute or relative reduction in vegetation height (ΔH: L-ratio = 2.67, df = 1, $P = 0.10$; ΔH_{rel}: L-ratio = 0.12, df = 1, $P = 0.73$). No significant interactions between vegetation height variables, grazing intensity (G) and size class (S) were found (df = 1 for all tests; HB × S: L-ratio = 0.5, $P = 0.5$; ΔH × S: L-ratio = 3.9, $P = 0.06$; ΔH_{rel} × S: L-ratio = 0.2, $P = 0.7$; HB × G: L-ratio = 2.6, $P = 0.1$; ΔH × G: L-ratio = 0.5, $P = 0.5$; ΔH_{rel} × G: L-ratio = 3.2, $P = 0.07$).

The G × S interactions were not significant for NG or BC (Table 2). The difference between low

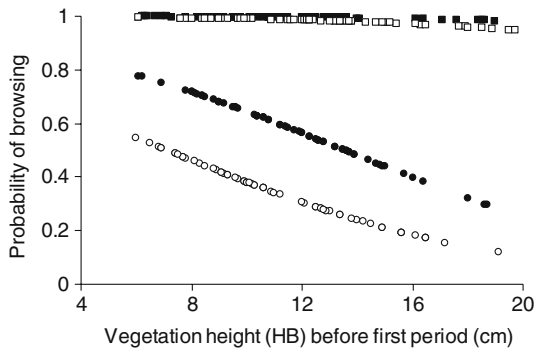

Fig. 3 Estimated probabilities (using logistic regression with a logit link) of each individual sapling being browsed as a factor of surrounding vegetation height (HB), controlling for effects of size class (○: small saplings and □: large saplings) and grazing intensity (*unfilled symbols*: low grazing intensity and *filled symbols*: high grazing intensity)

Table 2 Browsing experiment: likelihood ratio tests (*L*-ratio) for effect of grazing intensity (low and high), tree size class and their interaction (G × S) on relative new growth (log (NG + 1) and aboveground biomass change (log BC) of saplings

	Abies N = 45			*Picea* N = 48			*Acer* N = 50			*Fagus* N = 48		
	L-ratio	df	*P*	*L*-ratio	df	*P*	*L*-ratio	df	*P*	*L*-ratio	df	*P*
NG												
Grazing	0.01	1	0.92	1.43	1	0.23	4.5	1	< 0.05	2.33	1	0.13
Size	2.45	1	0.12	4.33	1	< 0.05	9.85	1	< 0.01	6.33	1	< 0.05
G × S	2.82	1	0.09	1.85	1	0.17	3	1	0.08	2.98	1	0.08
BC												
Grazing	0.23	1	0.64	0.01	1	0.98	8.43	1	< 0.05	0.31	1	0.58
Size	10.7	1	< 0.05	0.02	1	0.89	3.52	1	0.06	2.22	1	0.14
G × S	0.7	1	0.4	0.08	1	0.78	1.3	1	0.25	2.55	1	0.11

and high grazing intensity was significant only for *Acer* growth, but small saplings of all species tended to have greater NG under low grazing intensity (Fig. 4). For *Picea*, *Acer* and *Fagus*, small saplings produced relatively more new biomass than large saplings but aboveground biomass change did not differ significantly between sizes, except for *Abies*. In contrast to the evergreen species, all *Acer* and small *Fagus* saplings increased their aboveground biomass compared to their initial biomass under low grazing intensity, but not under high grazing intensity. Deciduous species were relatively less affected than evergreen species, which lost up to half of their initial biomass (Fig. 5).

Mowing experiment

The mowing treatment had no significant effect on NG and BC for either large or small saplings for any species (Table 3). Small saplings produced relatively more current-year shoots than large ones, except for *Abies* (Table 3, Fig. 4).

Combined analysis

The combined analysis provided evidence for significant reduction in growth due to cattle browsing compared to ungrazed control saplings although the effect was only marginally significant for BC of *Fagus*. One significant interaction was found for NG of *Acer* saplings (Table 4). Percentage reduction of new growth reached up to 99% for coniferous species (Table 5). For deciduous species the new growth reduction was lower (71%). Aboveground biomass was reduced on average with 54% for conifers and 22% for deciduous species compared to growth of saplings in ungrazed situations. It was relatively lowest for *Fagus* (6% for small saplings under low grazing intensity) (Table 5).

Discussion

The probability of a sapling being browsed depended on its size and the height of surrounding vegetation but not on its species. Saplings were more likely to be grazed early in the season under higher grazing intensity. By the end of the browsing experiment, only one large sapling but one quarter of the small saplings had escaped browsing. More frequent browsing of large saplings may be due to the greater apparency of saplings with more biomass. Similar effects have been found for other herbivores and tree species (Palmer and Truscott 2003; Renaud et al. 2003). Small saplings, which have smaller root systems, were more often uprooted and thus less persistent than large ones. However, uprooting occurred mainly after the first grazing period, when root fixation after transplantation was probably not yet complete.

The probability of the saplings of being browsed by cattle was lower when the surrounding vegetation height was high, as has been found elsewhere (De Steven 1991; Zamora et al. 2001). This protection tended to be more effective in the paddock subjected to the lower grazing intensity. If we suppose that the saplings were browsed by chance together with the surrounding vegetation, then the observed effect of vegetation height may

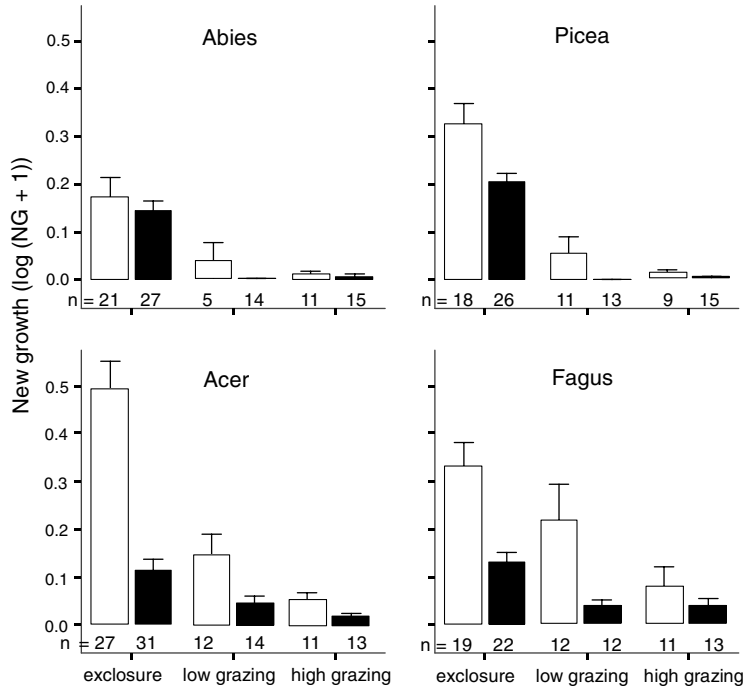

Fig. 4 Effect of grazing intensity (zero, low and high) and tree size class (*white bars*: small saplings; *black bars*: large saplings) on relative new growth (log (NG + 1)) (±1 SE) for each of the four tree species

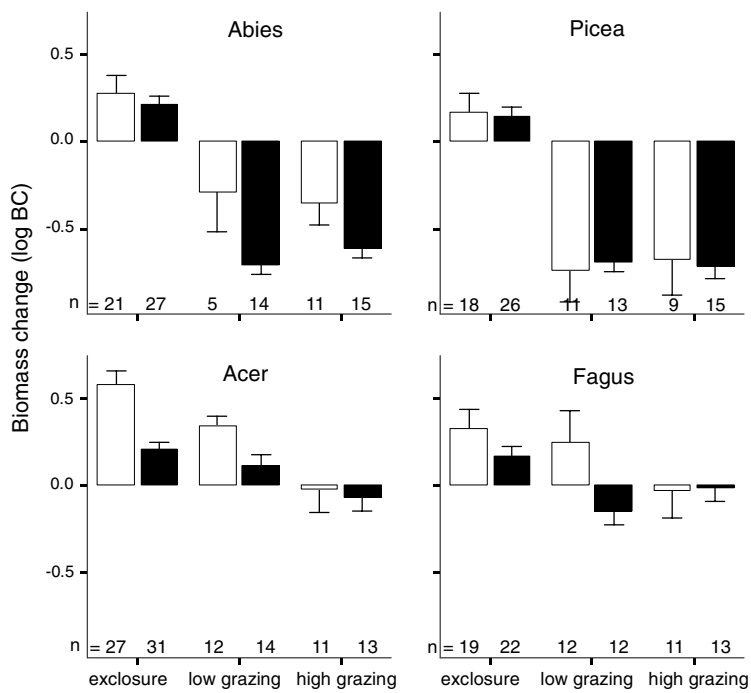

Fig. 5 Effect of grazing intensity (zero, low and high) and tree size class (*white bars*: small saplings, *black bars*: large saplings) on aboveground biomass change (log BC) (±1 SE) for each of the four tree species. Negative values correspond to biomass decrease, positive values to biomass increase

mean that (1) for morphological reasons the chance of a sapling being included in the bite is smaller when surrounding vegetation is taller or (2) cattle spent more time in patches where vegetation is short (WallisDeVries et al. 1999). Because cattle are primarily grazers (Gordon 2003), the rate of sapling discovery should depend on the perceived value of a particular patch in

Table 3 Mowing experiment: likelihood ratio tests (*L*-ratio) for the effect of mowing, tree size class and their interaction (M × S) on relative new growth (log (NG + 1)) and aboveground biomass change (log (BC)) of exclosed saplings

	Abies N = 48			*Picea* N = 44			*Acer* N = 58			*Fagus* N = 41		
	L-ratio	df	*P*	*L*-ratio	df	*P*	*L*-ratio	df	*p*	*L*-ratio	df	*P*
NG												
Mowing	0.87	1	0.35	0.38	1	0.54	0.37	1	0.54	0.97	1	0.33
Size	0.65	1	0.42	7.38	1	< 0.01	32.6	1	< 0.0001	14.3	1	< 0.0001
M × S	0.48	1	0.49	0.68	1	0.41	0.56	1	0.45	0.13	1	0.72
BC												
Mowing	0.78	1	0.38	0.24	1	0.62	0.27	1	0.61	0.64	1	0.42
Size	0.42	1	0.51	0.01	1	0.93	17.4	1	< .0001	1.76	1	0.18
M × S	0.22	1	0.64	0.40	1	0.53	0.14	1	0.72	0.05	1	0.82

Table 4 Combined analysis: likelihood ratio tests (*L*-ratio) for grazing intensity (zero, low, high), for tree size class and their interaction (G × S) on relative new growth (log (NG + 1)) and aboveground biomass change (log BC) of saplings

	Abies N = 93			*Picea* N = 92			*Acer* N = 108			*Fagus* N = 89		
	L-ratio	df	*P*	*L*-ratio	df	*P*	*L*-ratio	df	*P*	*L*-ratio	df	*P*
NG												
Grazing	23.7	2	< 0.0001	38.9	2	< 0.0001	23.3	2	< 0.0001	11.9	2	< 0.05
Size	1.07	1	0.3	10.2	1	< 0.05	36.3	1	< 0.0001	19.5	1	< 0.0001
G × S	0.33	2	0.85	4.19	2	0.12	21.3	2	< 0.0001	4.60	2	0.1
BC												
Grazing	40.1	2	< 0.0001	24.3	2	< 0.0001	22.1	2	< 0.0001	5.20	2	0.07
Size	6.24	1	< 0.05	0.01	1	0.93	19.1	1	< 0.0001	3.93	1	< 0.05
G × S	3.60	2	0.17	0.11	2	0.95	4.65	2	0.09	2.93	2	0.23

Table 5 Percentage reduction in relative new growth (%NG) and aboveground biomass change (%BC) of small and large saplings exposed to low and high grazing intensities

	Low grazing		High grazing	
	Small	Large	Small	Large
%NG				
Abies	80	99	95	95
Picea	84	99	97	99
Acer	76	61	92	83
Fagus	33	72	79	72
%BC				
Abies	43	61	48	57
Picea	56	57	55	57
Acer	26	10	44	24
Fagus	6	26	27	16

%BC = [(mean BC_control – mean BC_grazing) × (mean BC_control)$^{-1}$] × 100 and %NG = [(mean NG_ control – mean NG_grazing) × (mean NG_control)$^{-1}$] × 100

which the sapling is located. If the neighbourhood of the tree sapling is attractive, they are more likely to be browsed (Rousset and Lepart 2003). Tree regeneration has been shown to occur most often in safe sites (Harper 1977), such as on rocky outcrops or near unpalatable plants providing protection against browsers (Callaway et al. 2000; Milchunas and Noy-Meir 2002; Bakker et al. 2004; Smit et al. 2005).

Overall, browsing reduced both the biomass of current-year shoots and total aboveground biomass for all tree species and size classes. In addition to being browsed, almost all large saplings showed clear basal scarring due to trampling (C. Vandenberghe personal observation) (cf. Pitt et al. 1998), but none of the saplings were broken. This study was conducted under unusually dry weather conditions and the amount of browse consumed by cattle is likely to vary with weather conditions and forage availability (Pollock et al. 2005). Although statistically significant only for *Acer*, all small saplings tended to have a higher new growth production under low grazing intensity than under high grazing intensity, as has been found for birch saplings exposed to sheep grazing

(Hester et al. 1996). Although small saplings escaped more often browsing than large ones, they did not show in all cases a lower relative reduction in biomass (Table 5). Small saplings lost relatively a larger proportion of biomass when effectively browsed than large ones.

The evergreen species we used lost relatively more biomass when browsed than the deciduous species. The larger reduction was presumably due to a more vulnerable plant architecture and the attractive abundant fresh foliage at the start of the summer (Welch et al. 1991). Moreover, deciduous species may more quickly compensate for mammalian herbivory by mobilising stored energy reserves from stem and roots for refoliation (Chapin et al. 1990; Hester et al. 2004). Small *Fagus* saplings seemed to be less reduced in biomass when exposed to browsing than the other species. This might be partly explained by a lower browsing frequency during the first grazing period (Fig. 4), allowing more biomass production before being damaged. The differences in biomass losses do not necessarily imply a lower survival rate for conifers although tolerance to defoliation is generally greater in deciduous than coniferous species (Krause and Raffa 1996). The performance of the deciduous species may decline in later growing seasons, especially if their resources have been depleted to compensate for damage but also due to repeated browsing.

Unexpected findings emerged from the mowing experiment since reducing aerial biomass around the saplings did not affect sapling growth. Competition for light between grasses and planted tree saplings may have been outweighed by belowground competition for resources. In contrast, Gill and Marks (1991) found that aboveground competition with herbs reduced tree sapling growth more severely than belowground competition. In their study, water was not a limiting factor which may have increased the relative importance of light. The extremely warm and dry weather conditions during the growing season of 2003 may have increased the importance of water and thus weakened the effect of light competition. As suggested by Nilsson and Örlander (1995), after they found no effect of sward mowing on *Picea* sapling growth, the evaporative demand of the planted saplings may have been higher in mown plots since control saplings were partly shaded. Furthermore, mowing may have altered the availability of other resources such as soil nitrogen (Holland and Detling 1990) and understanding the multiple effects of mowing will require further experiments. In addition, the duration of our experiment (3 months) may not have been long enough to detect competition effects. Browsing and plant competition interactions might be expected (see Husheer et al. in press) because the reduction of aboveground surrounding vegetation by herbivores may also increase the probability of being browsed (Canham et al. 1993; see above) and/or affect browsing tolerance (Weltzin et al. 1998; Wise and Abrahamson 2005).

We have showed that browsing frequency depends on the tree size and the height of surrounding vegetation but not on species. Cattle browsing reduced tree sapling growth of the four most common tree species of the wooded pastures in the Swiss Jura Mountains. The differences in browsing frequency and sapling growth between low and high grazing intensities were moderate. At least in the short term, the deciduous species were less affected in aboveground growth and thus more tolerant at this particular stage than the evergreen species. In order to survive, tree saplings must be browsing tolerant, i.e. they should be able to persist at least temporarily with reduced biomass and to compensate for biomass loss through active regrowth. To determine which species is most tolerant over longer terms, we are studying the effects of herbivory on whole-sapling growth and survival in an experiment currently underway.

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